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AND ITS BEARING ON THE THEORY
OF PURE GAMETES

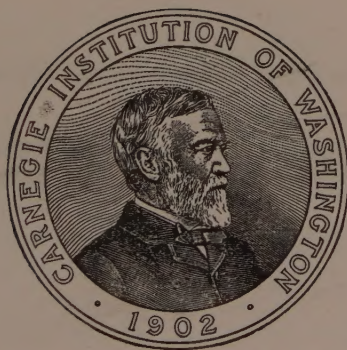
BY

W. E. CASTLE AND ALEXANDER FORBES

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OF GUINEA-PIGS

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PAPERS OF THE STATION FOR EXPERIMENTAL EVOLUTION AT COLD SPRING HARBOR,
NEW YORK, No. 5

CONTRIBUTIONS FROM THE ZOÖLOGICAL LABORATORY OF THE MUSEUM OF COMPARATIVE
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5. HEREDITY OF HAIR-LENGTH IN GUINEA-PIGS, AND ITS BEARING ON THE THEORY OF PURE GAMETES.

By W. E. CASTLE AND ALEXANDER FORBES.

1. INTRODUCTION.

In earlier papers (Castle, :03, :05) it has been shown by one of us that long or "Angora" coat in guinea-pigs and rabbits is alternative in heredity to normal or short coat. It has been shown further that in cross-breeding normal or short coat dominates over long coat, in conformity with Mendel's law of heredity, but that the purity of the gametes formed by cross-breds is not absolute. Impurity of the gametes is indicated by two facts: First, the number of long-haired young produced by cross-bred parents is in excess of the Mendelian proportion, one-fourth; secondly, many of these long-haired young show an imperfect development of the long-haired character, as compared with their long-haired ancestors. Both these facts may be explained by supposing that the alternative characters, short and long hair, which are present in the cross-breds—one seen, the other unseen—have in many cases failed to segregate, or have segregated only imperfectly, when gametes have been produced by the cross-breds. Accordingly the conformity with Mendel's law is a qualified one.

More extended and detailed studies made by us during the past year confirm these conclusions and add several new facts concerning the behavior in heredity of these alternative characters. The idea advanced tentatively by Castle (:05), that the hair-lengths of guinea-pigs form a discontinuous series of two, three, four or more times the length of short or normal hair, is found to be incorrect. Careful examination of the hair of several hundred guinea-pigs (mostly cross-breds) shows that there occur hairs of practically all lengths from 3.3 cm. up to about 23 cm. The series of supposed maximal hair-lengths of twice 4 cm., thrice 4 cm., etc., resulted from an insufficient number of observations.

2. CHARACTER OF FOLLICLE ACTIVITY IN THE PRODUCTION OF SHORT AND OF LONG HAIR.

If an examination is made of the longest hairs plucked from the back of an adult short-haired guinea-pig, it is found that the hairs narrow toward the base, owing to a diminution in the diameter of the medulla, which is entirely wanting in the follicle (see Fig. 1, *A*). Such a hair has ceased to

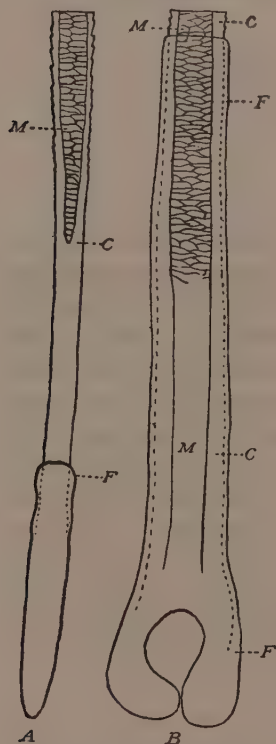


FIG. 1.—*A*, Base of hair, fully grown, of determinate growth type.

B, Base of hair of indeterminate growth. From camera drawings, same magnification.

C, Cortex; *F*, follicle; *M*, medulla.

grow, having completed a definite growth cycle, and will sooner or later be shed. This growth cycle was nearing its end when the follicle ceased to form medullary substance. In ordinary guinea-pigs the hair stops growing when it has reached a length of about 4 cm. In long-haired guinea-pigs the hair-follicle does not cease forming medullary substance when a definite hair-length has been attained. The growth of the hair is indefinite, ending only with the degeneration of the follicle itself. The time when this occurs is determined to some extent by the physical condition of the animal. The lifetime of a hair-follicle of this sort may be prolonged by good care, as fanciers well know. Pregnant or nursing mother guinea-pigs frequently lose their longest hair. Insufficient or improper food is likely to have a similar result in either sex. Accordingly, the fancier gives careful attention to the diet of long-haired animals intended for exhibition, and often protects the hair in special ways from mechanical injury. There is, however, no reason to suppose that such care induces indefinite activity of the hair-follicle. On the contrary, animals of a short-haired race, under the best of care, will form only hairs of determinate length, whereas animals of a long-haired race, however much abused, will, so long as they live, continue to form hairs of indeterminate

growth. The two types of hair-growth are quite distinct, and are sharply alternative in heredity. They are probably paralleled in our own head- and body-hairs respectively, the former being of indeterminate, the latter of determinate growth.

Like ourselves, long-haired guinea-pigs bear hairs of both sorts, whereas short-haired guinea-pigs, like our probable simian ancestors, bear only hairs of determinate growth. Similar alternative conditions of hair-growth occur in many different kinds of mammals, as for example in rabbits, goats, cats and horses, the indefinite growth in the latter case occurring in the hairs of the mane and tail only (see Davenport, :04). The long-haired (or indefinite growth) condition is doubtless cœnogenetic in all cases, and has probably arisen independently in each case as a discontinuous variation or mutation. By selection the long-haired condition is easily made a racial character, for long-haired animals produce only long-haired offspring. But without selection, what would be the fate of this mutation? This our breeding experiments may perhaps indicate.

Let us consider first the extreme conditions of follicle activity which we have encountered in the guinea-pigs studied. In long-haired guinea-pigs the hairs all over the body attain a greater length than in short-haired ones, but only hairs of the back and sides grow indefinitely. Accordingly, in comparative studies of the hair-length, it has been found convenient to select a few of the longest hairs to be found on the back or rump of the animal and to use these as a standard of comparison. Following this method the hair of guinea-pigs of different races has been measured at frequent intervals from birth to an age at which the hair had attained full growth.

A litter of four guinea-pigs of a pure short-haired race yielded measurements which combined are expressed graphically in Fig. 2, *A*. Starting at birth with a length of about 18 mm., the hairs grew very rapidly during the first week, at the end of which they measured about 25 mm., an average increase of a millimeter a day; in the second and third weeks they grew less rapidly, measuring about 29 mm. at the end of two weeks, and 33 mm. at the end of three weeks. At this time the growth of the hairs which the animals bore at birth was practically complete; the hair-follicles now ceased to form medullary substance, and consequently the hair narrowed to a base of solid cortex (Fig. 1). From this time on the measurements show from week to week only slight deviations from a length of 33 to 35 mm.

Several series of measurements of the hair of long-haired guinea-pigs, when combined and expressed graphically, are shown in *D*, Fig. 2. The hair-length at birth is about the same as in animals of class *A*, or even a little shorter, but the growth rate does not show the series of rapid changes seen in class *A*. Growth progresses very steadily at an average rate of about 0.83 mm. a day during the first one hundred days and at about 0.75 mm. a day during the second one hundred days. But a glance at Fig. 2, *D*, shows that the slowing up of the growth rate is a very gradual process.

After the hairs have attained a length of about 170 mm. they begin to fall out, but without previously narrowing to a base, as in class *A*. Rarely does a

hair attain a length of 200 mm. As the longest hairs are shed, new ones are found to be growing up to take their places, but there is usually a period, after shedding sets in and before the second-growth hairs are fully developed, when the maximum coat length shows a decided falling off. This is indicated in *D*, Fig. 2, as occurring at about the age of two hundred and fifty days. The type of hair growth found in class *D* may be called *indeterminate* or continuous; that of class *A*, *determinate*.

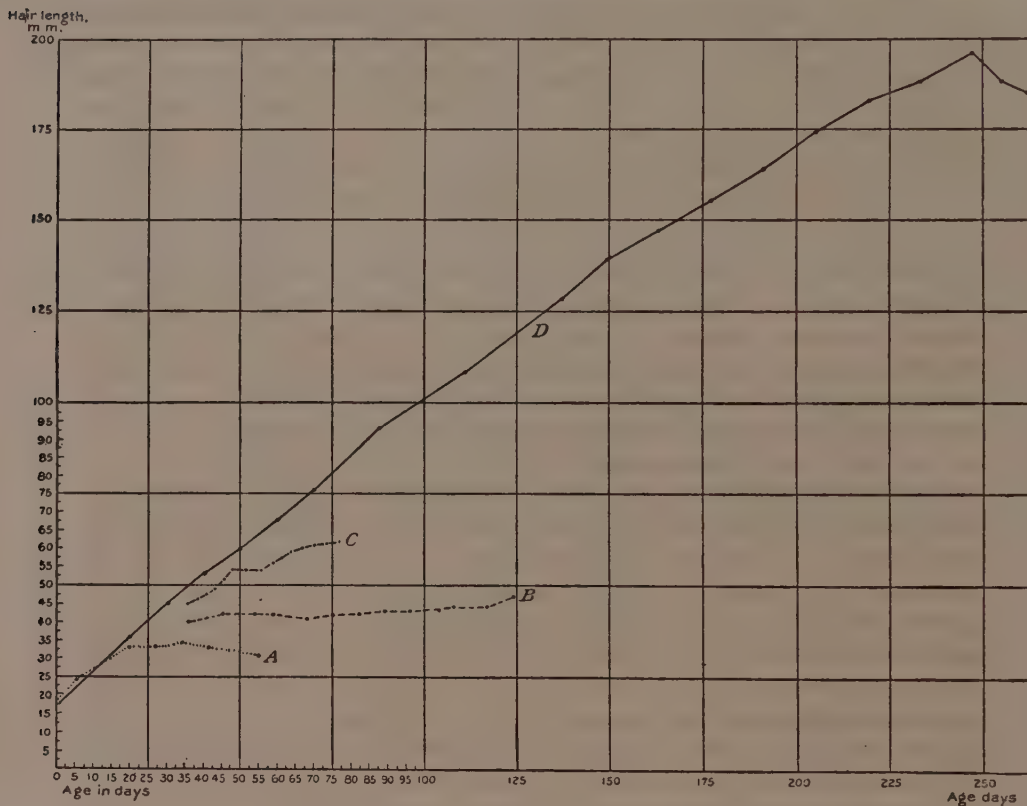


FIG. 2.

Our original stock of short-haired guinea-pigs showed considerable variation in maximal hair-lengths, ranging from 35 to 50 mm., but all of the determinate type of growth (classes *A* and *B*, Fig. 2). The great majority of them would probably have fallen in class *B*, but we can not be sure of this, as many of the animals were no longer available for record when we began making hair-measurements systematically. The hair-lengths recorded for class *A* are certainly exceptionally short, even for animals of determinate hair growth.

3. THE EFFECTS OF CROSS-BREEDING BETWEEN SHORT-HAIRED AND LONG-HAIRED ANIMALS.

(a) MATING $B \times D$.

When the short-haired animals were mated with animals of class D , only young of the former sort were obtained, which result shows clearly the dominant character of short hair. However, the maximal hair-length of the cross-breds was usually 40 to 50 mm. (class B , Fig. 2); that is, it fell within the *upper* half of the range of variation of the pure short-haired stock, though in no case, we think, did it transcend the range of variation of the short-haired stock itself. We are warranted, then, in concluding that the dominance in the offspring of the short-haired type of growth is complete. Type B mated with type D gives only type B .

(b) MATING $B(D) \times B(D)$.

But when cross-breds between the types B and D were bred together, not only did type D reappear after skipping a generation, but a new and intermediate type was found also, which we may call type C . This is not sharply separated from types B and D , but is made up of individuals scattered all the way between those parental types. It contained, first, individuals whose hair grew continuously from the age of twenty days on, but much more slowly than does the hair of class D , with a tendency to break off at lengths much less than those attained in class D . The long hairs of such animals were also frequently less numerous than in typical class D , as if *part* of the hairs only were continuous in growth, while the others were determinate. In these individuals we see the alternative characters coexisting as in a mosaic. In other cases animals placed in class C appeared to have only hair of determinate growth, but growth continued until a length of 60 to 80 mm. had been attained before the hair narrowed to a base. Such animals represent an intimate blend rather than a mosaic of the contrasted types B and D , yet with a closer approximation to type B ; but no sharp line could be drawn between the blends and the mosaics, as the two graded into each other and into the two parental types. These intermediates (class C) were about as numerous as the animals of type D , but only about half as numerous as those of type B . Thus, in a particular experiment there were produced twenty-nine B , twelve C and ten D individuals, together with eleven of unknown character, because they died or were disposed of before their hair was fully grown. The grandparents of this lot were the long-haired male, 2002 (Castle, :05, Pl. 1, Fig. 1), and several different short-haired females; the parents were all of class B . The Mendelian expectation

from an experiment like the foregoing is that there will be produced three times as many animals of type *B* as of type *D*, or in a total of fifty-one young (the number whose character was definitely ascertained) thirty-eight *B* to thirteen *D*. Comparing with these numbers the observed ones (twenty-nine *B* and ten *D*), we notice that there are fewer individuals than expected in each of the classes *B* and *D*, from which we may conclude that each has contributed to the formation of the intermediate class *C*. The hypothesis on which the Mendelian expectation rests is this, that each cross-bred animal will form in equal numbers gametes bearing the pure *B* character and the pure *D* character respectively. Evidently from this experiment it follows either that some of the expected *B* and *D* gametes are not pure, or else that in this generation the result of a union between a *B* and a *D* gamete is not the same as in the original cross. In either case we are forced to admit *modification* of gametes from their original pure condition.

In two other families of guinea-pigs, cross-breds mated *inter se* produced a result similar to that already described. The young in these families were classified as nine *B*, five *C*, two *D* and four undetermined. These cases differ from the foregoing in that, in producing the cross-breds used, *two* crosses with the *B* race were made to one with the *D* race, whereas in producing the first mentioned lot of cross-breds the *B* and *D* stocks were equally represented in the ancestry. It is perhaps significant that the *D* young are relatively fewer in these families, though the total is too small to allow one to attach much importance to the proportions observed among the young.

(c) MATING $B(D) \times D$.

On the Mendelian hypothesis of pure gametes, this cross should yield classes *B* and *D* in equal numbers. In matings in which three different *D* males were employed, it has produced fourteen *B*, seventeen *C* and nineteen *D* offspring, together with five of undetermined character. Since *D* parents are known to form only *D* gametes, it seems clear from this experiment that the hybrid, or $B(D)$ parent, formed gametes a considerable number of which bore the intermediate or *C* character. If a single cross of *D* with *B* has such an effect in modifying gametes, a repetition of the cross should have a still more marked influence, producing a still larger proportion of intermediate or *C* gametes. The mating next to be described bears on this question.

(d) MATING $B(D)$ [FROM TWO SUCCESSIVE CROSSES WITH *B*] $\times D$.

Three different *D* males were used in making this cross. They produced thirty-two *B*, thirty-seven *C*, and twenty-nine *D* offspring, together with seven of undetermined character. Here the *C* class is actually larger

than either of the others, though the increase over the last mating is not a very striking one, and several individuals were just on the line between *C* and *D*, so that little stress can be laid upon the classification made.

(e) MATING *B(D)* [FROM TWO SUCCESSIVE CROSSES WITH *D*] \times *D*.

If two crosses introduce greater contamination of the gametes than one, then the *C* and *D* classes resulting from this cross should be high at the expense of the *B* class. The observed result accords with this interpretation, though the number of young produced is not large. There were one *B*, three *C* and five *D* offspring.

The question now arises, What is the nature of the *C* individuals? Are they the result of partial reversal of dominance, so that when *B* meets *D* in fertilization there is produced an intermediate condition, or have *B* and *D* actually fused to form something different from either? Matings of *C* individuals among themselves or with *B* and with *D* respectively should throw light on this question. If *C* individuals result merely from partial arrest of the dominance of *B*, we shall expect *C* to split at gamete formation into *B* and *D*. If it does not do this we may conclude that it represents a firm union of *B* and *D* to form a new character, *C*.

(f) MATING *C(D?)* \times *D*.

This mating produced a mixture of *C*'s and *D*'s, in all eight *C*, nine *D* and five individuals of undetermined character. Apparently the *C*'s used in this experiment were heterozygous, producing some *C* and some *D* gametes. The former, combined with *D* gametes, produced *C* individuals; the latter similarly united produced *D* individuals. The fact that no *B* offspring were produced indicates that the *C* parents did not form *B* gametes. We conclude that the *C* gamete is probably a new creation due to a partial and permanent blend of *B* with *D*.

(g) MATING *C(D)* [PRODUCED BY TWO SUCCESSIVE CROSSES WITH *D*] \times *D*.

This mating should yield a larger proportion of *D* offspring than the last, if cross-breeding introduces contamination of gametes. The observed result was nine *C*, eighteen *D* and six young of undetermined character, which result supports the hypothesis stated. It should be said that in this mating, as in those previously described, the classification of the offspring was wholly unbiased, as it was in each case made before the animal's pedigree was looked up to see in what group of offspring the individual in question should be placed. It must be borne in mind, however, that the *C* group is not a natural one to be considered a unit-character by itself. It

is simply a poorly developed *D*, *C* and *D* being grades, arbitrarily fixed, of the continuous growth type of hair. Or, if we think of *C* as a synthesis of *B* with *D*, then this *C* partakes more largely of the character of *D* the more often the parental *B* has been crossed with *D* in its production. From the fact that the *C* parents give off gametes partaking in different degrees of the *D* character, it seems probable that the synthesis of *B* and *D* to form *C* has been as yet imperfect, as of two ingredients incompletely mixed together, so that different samples contain different proportions of the *D* character. This view is supported by the result obtained by mating *C* with *C*, but as the parents used in this experiment were of different origin from those mentioned in the foregoing pages, it may be well first to describe the source from which they came.

4. ORIGIN OF RACE *C'*, AND RESULTS OF CROSSES IN WHICH IT WAS EMPLOYED.

A family of short-haired guinea-pigs (class *B*), when inbred, produced a few individuals with hair about twice as long as that of their parents. The long hairs were not very numerous. It seems probable, in the light of subsequent studies, that only a few of them were continuous in growth, the others being determinate, but attaining a greater length than do ordinary hairs before growth ceased. When two of these long-haired animals were mated together, all the offspring were long-haired, though some of them had more numerous long hairs than others, or hairs of a greater maximum length. By selecting the best long-haired individuals for two generations a race of imperfectly long-haired individuals was produced, of about the same degree of excellence as the group *C* already described, which was produced by cross-breeding between *B* and *D*. To distinguish it from the latter, we may call this race *C'*.

The *C'* race, bred by itself, produced no *B* individuals, though the maximal hair lengths obtained varied considerably. This result shows clearly that no *B* gametes were produced by the *C'* race, though it had just arisen from the *B* race, in which very likely it had previously been present as a recessive character.

A mating between *C'* and *D* gave a mixture of *C* and of *D* individuals, the two classes being about equally numerous (seven *C* to five *D* in one set of experiments). Certain individuals, however, were just on the line between the two classes, so that no great importance can be attached to the proportions observed. But the result does show, what breeding *C* or *C'* individuals *inter se* had shown, a considerable degree of variability among the *C* and *C'* gametes, this variability being a sufficient basis for selection for increased hair-length. While, accordingly, the variation made its appearance as a discontinuous one, it showed itself amenable to selection.

5. GAMETES OF CROSS-BREDS OFTEN IMPURE.

From the foregoing observations it is clear that, while the long-haired and short-haired conditions are sharply alternative to each other in heredity, the gametes formed by cross-breds are not in all cases pure. Frequently they consist of a blend or a mixture of the two alternative conditions, constituting in effect a new condition intermediate between the other two. A study of other characters alternative in heredity yields results somewhat similar.

Albinism is, in heredity, the most sharply alternative of characters, yet cross-breeding between albino and pigmented guinea-pigs may modify the character both of the albino race and of the pigmented one. This modification may take on a variety of forms, as has elsewhere been pointed out (Castle, :05). It may result in the production of mosaics (pigmented animals spotted with white), or of albinos with a modified peripheral pigmentation, or of albinos visibly like their ancestors but transmitting a different set of latent characters. Again, the rough or rosetted coat of certain races of guinea-pigs is sharply alternative to smooth coat, yet cross-breeding of rough with smooth races may induce curious modifications of the rough character or produce smooth individuals bearing the merest trace of the rough character.

All these facts are in harmony with the hypothesis, for which there is strong evidence on the cytological side, that each separately heritable character is represented by a different structural element in the germ (egg or spermatozoon). In fertilization the paternal and maternal representatives of a character become more or less closely united, this union persisting through all subsequent cell-generations until the new individual forms its sexual elements. At that time the paternal and maternal representatives of a character separate from each other and pass into different cells.

But the paternal and maternal representatives of a character may in the meantime have exercised on each other a considerable influence. In the case of some characters, as ear-length in rabbits (Castle, :05^a), they completely blend and intermingle, so that a new character is produced strictly intermediate between the conditions found in the respective parents.

In other cases the modification may be slight, as if the paternal and maternal representatives of a character had been scarcely more than approximated. Sometimes in cases of alternative inheritance no influence of the cross is observable in certain of the "extracted" individuals, but if any considerable number of individuals is examined, others will be found in which the cross-breeding manifests its influence. From this we conclude that gametic purity is not absolute, even in sharply alternative inheritance.

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6. THE ORIGIN OF A POLYDACTYLOUS RACE OF GUINEA-PIGS.

By W. E. CASTLE.

1. FIRST APPEARANCE OF THE POLYDACTYL CHARACTER.

Normal guinea-pigs have four toes on each front foot but only three on each hind foot. The race of guinea-pigs whose origin is to be described differs from ordinary guinea-pigs in possessing four digits on each hind foot instead of three. The four digits of the front foot apparently correspond with digits 2-5 of the typical five-fingered appendage, while the three digits of the hind foot correspond with digits 2-4 of the typical appendage. In other words, all guinea-pigs have lost from the front foot the digit which corresponds with our thumb, and normal guinea-pigs have lost from the hind foot two digits, which correspond respectively with our "great" and "small" toes. In the race to be described the "small toe" is present on the hind foot as well as on the front.

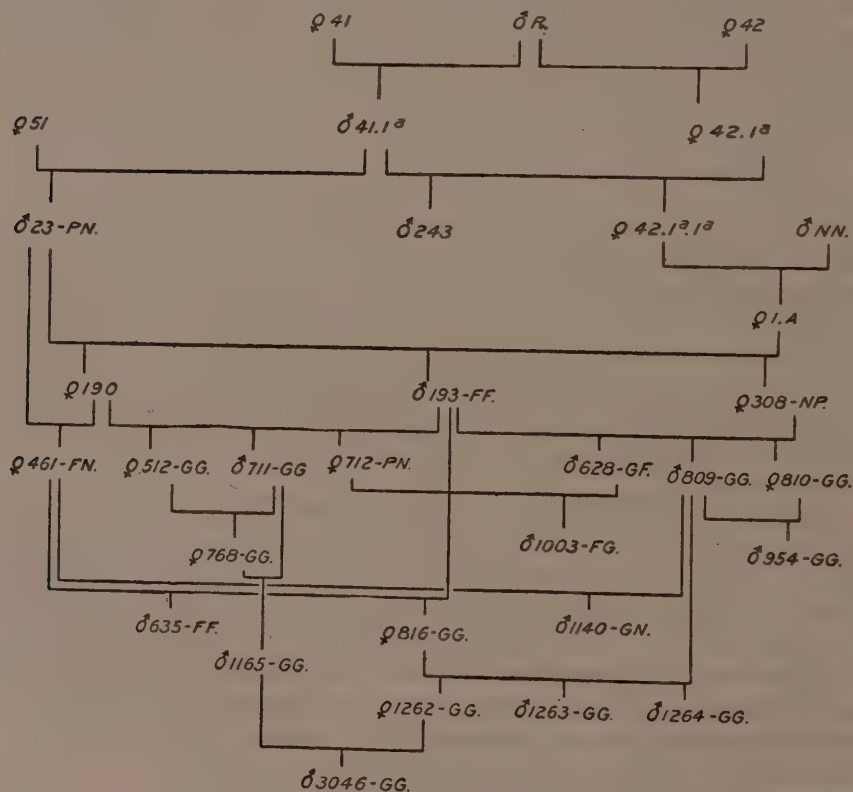
In October, 1900, several ordinary guinea-pigs were obtained from a nearby breeder, one pair of which produced in the following June three male young. The largest of these young bore an imperfectly developed digit on its left hind foot, in the position of a "small toe." This toe bore a well-developed claw and apparently contained the bony phalanges, but these evidently were not joined with the foot by appropriate muscular and tendinous connections, for the toe hung limply down from the side of the foot like a bag of skin. It remained attached to the foot until the animal was fully grown, but was then lost, probably having been accidentally pulled off.

Previous to the birth of this polydactylous guinea-pig, I had never seen a fourth digit on the hind foot of a guinea-pig, nor heard of its occurrence either among wild or domesticated Caviidæ, and I am unable to find any reference to such a character in the literature of the group. But I have since found that the "extra-toe" does occur not infrequently among guinea-pigs in an imperfectly developed condition, and I have twice since obtained animals of this sort from breeders. From the progeny of the single polydactylous individual born in June, 1901, a well-established race of four-toed guinea-pigs has now been formed. An account of how this was done, it is hoped, may be of value as bearing on the origin of breeds.

The original polydactylous guinea-pig ($\sigma^7 23$, table 1, p. 18), was born to parents of almost unknown ancestry, but certainly not closely related to each other. The mother, a spotted animal ($\text{Q } 51$) produced no other polydactylous offspring, though she bore in all thirty young. But the father ($\sigma^7 41.1^a$), who sired in all one hundred and forty-seven young, had five other polydactylous offspring. These were all, except one,* borne by females descended from himself, and that one was borne by his half-sister ($\text{Q } 42.1^a$), so that it seems certain that the polydactylous character came in every case from the same individual, $\sigma^7 41.1^a$. A son of $\sigma^7 41.1^a$ —viz, $\sigma^7 243$ (table 1)—whose mother was half-sister to $\sigma^7 41.1^a$, produced, like his father, a certain number (five) of polydactylous offspring, which were used in building up the polydactylous race.

TABLE 1. — *Ancestry of the various males used in building up the polydactylous race.*

The character of the extra-toe is indicated by letters following the numeral which designates each individual. These letters signify: *G*, good; *F*, fair; *P*, poor; *N*, normal, *i. e.*, three-toed. Read downward.



* In an earlier paper (Castle, :05) this exception was inadvertently overlooked, and the total number of young sired by $\sigma^7 41.1^a$ was given as 139 instead of 147.

2. PROGENY OF THE ORIGINAL POLYDACTYLOUS INDIVIDUAL.

The polydactylous male (σ 23), in a total of seventy-seven young, produced fifteen polydactylous ones. The proportion of polydactylous individuals varied much among the offspring by different mothers. (See table 2.) Unrelated mothers, from families in which polydactylism had not been observed, gave only two polydactylous young to thirty normal ones, or 6.25 per cent. polydactylous. *Related* normal mothers—that is, mothers descended from σ 41.1^a—gave nine polydactylous to twenty-seven normal, or 25 per cent. polydactylous, while polydactylous mothers gave four polydactylous to five normal young, or 44 per cent. polydactylous young.

Many of the young of σ 23 had the extra digit present on both the right and the left hind feet, and in several of these the digits were better developed than in the father, evidently with all the appropriate muscles necessary for functional toes. One of the best of these young was σ 193 (table 1). His mother was a normal individual descended from σ 41.1^a, but gave a larger proportion of polydactylous young than any other mother had done up to that time. By σ 23 she had five polydactylous and six normal young.

To express the degree of development of the extra digit a series of three grades was now established, *good*, *fair* and *poor*, which will be abbreviated to *G*, *F* and *P* respectively. *Good* means a fully developed and functional fourth toe; *fair* means a fourth toe rather smaller than the others, often turned upward a little in walking, as if its muscular equipment were imperfect; *poor* means a loosely hanging toe, either with or without a nail; sometimes the toe described as *poor* is represented by only a soft fleshy bag of skin attached to the side of the foot, without either nail or hair, destined to shrivel up and drop off within a few days after birth. In distinction from these three classes, the term *normal* (*N*) will be used to describe a three-toed foot. In describing the condition of the toes of an individual, the left foot will always be named first; thus *GP* will mean an individual having a good fourth toe on the *left* foot, a poor one on the *right* foot.

3. PROGENY OF THE SECOND POLYDACTYLOUS GENERATION.

Male 193, as regards the extra-toe, was classed as *FF*, but he produced about fifteen young with well-developed extra-toes, which placed them in class *G*. About one-fourth of all his polydactylous young were of this sort, the polydactylous including more than half his young (forty-eight out of eighty-six).

METHOD OF GRADING THE PROGENY.

Of course the female mates of ♂ 193 were in many cases superior in toe development to the mates of his father, ♂ 23, though in many cases they were identical. Accordingly it is necessary, in estimating the respective potency of the two animals, to separate the mothers into groups of similar toe development, or of similar pedigree when no extra-toes were present. Consequently, five groups of mothers have been made (see tables 2-14), viz, *G*, *F*, *P*, *N* and *N'*. Group *G* includes only mothers having well-developed extra-toes on both feet (*GG*); *F* includes mothers having fairly well-developed toes, or with one good toe only (*FF*, *FG*, or *GF*); *P* includes mothers with at least one toe poorly developed (*P*); the other toe may be fair or poor, or the foot may be normal. *N* includes normal (*NN*) mothers descended from ♂ 41.1^a or nearly related to him; *N'* includes normal mothers not descended from ♂ 41.1^a, but belonging to families in which, when inbred, polydactylism does not occur.

When the mothers are grouped in this way, we find, first, that the proportion of polydactylous young produced by a male decreases in the successive classes from *G* to *N'*; and secondly, that the degree of development of the toes produced on those polydactylous young diminishes in the same order.

It would manifestly be unfair in estimating the potency of transmission in a given case to omit either of these considerations—the proportion of polydactylous young, or the degree of development of their extra-toes. So an attempt has been made to combine the two into a numerical grade for the young by each group of mothers. This grade is given in the last column of tables 2 to 14. In making up the grade each *G* toe counts 100, each *F* toe 80, and each *P* toe 50, while *N* counts 0. The total thus obtained for a group of young is divided by twice the total number of young in that group, that is, by the whole number of feet which *might* bear the extra-toe. Measured by this standard, a group of young, *all* of which had the extra-toe well developed on both hind feet, would be graded 100; a group of young with no extra-toes would be graded 0, while mixed groups would come in between 0 and 100. A group of young averaging *P* would be graded 50, and a group averaging *F* would be graded 80.

Comparing the young of ♂ 193 (table 3) with those of his father, ♂ 23 (table 2), we see a marked increase in the potency of transmission of the extra-toe within the same group of mothers. The grades of the young produced by the last four groups of mothers (*F* to *N'*) in the case of ♂ 23 are 29, 19, 17, and 1.5, respectively, while in the case of ♂ 193 they are 58, 57.5, 22 and 18.5.

4. PROGENY OF THE THIRD POLYDACTYLOUS GENERATION.

Continuing to trace the history of the polydactylous race in the male line, we may notice that the sires of the next generation of young consisted of four sons of ♂ 193. Two of these were own brothers, viz, ♂ 628 and ♂ 809 (see table 1). The other two were half-brothers to these two and to each other. They were ♂ 635 and ♂ 711. The young of these four males are classified as regards the extra-toe character in tables 4 to 7 (see pages 25 and 26). An examination of these tables shows for ♂ 809 an increase of potency over that of his father, ♂ 193; ♂ 711 shows a potency very similar to that of his father, but the other two males, ♂ 628 and ♂ 635, are clearly inferior to their father in potency, their average grades being about 34 and 38 respectively, while that of their father was 46.

5. PROGENY OF THE FOURTH POLYDACTYLOUS GENERATION.

The sires of the next generation consisted of six males, four of which were sons of the best male (809) of the previous generation, while one was a son of ♂ 628, and one a son of ♂ 711. Considering first the four sons of ♂ 809 (table 7), we notice that three of them, ♂ 954 (table 8), ♂ 1140 (table 10) and ♂ 1264 (table 13), are clearly inferior to their father in potency. The fourth male, ♂ 1263 (table 12), makes a somewhat better showing than his father, though two of the possible groups of mothers (*F* and *N*) are wholly unrepresented among his mates and their values can only be roughly estimated by interpolating values, while two other groups are very inadequately represented. Yet all the data available agree in showing high potency on the part of this male. Out of a total of eighty-three young which he has sired, only one has been three-toed.

Male 1003 (table 9) has a record similar to that of his father, ♂ 628 (table 4), but on the whole better. It is noteworthy that neither of these animals gave polydactylous offspring when mated to unrelated normal females, though by polydactylous mothers they had a good proportion of polydactylous young.

Male 1165 (table 11), also, has a record like that of his father, ♂ 711 (table 6). By unrelated normal (*N'*) females he produced offspring grading 10 as regards the extra-toe character, his father's offspring by the same group of mothers grading 8. By matings with polydactylous mothers, both father and son have produced offspring grading below those of ♂ 809 and of ♂ 1263.

6. PROGENY OF THE FIFTH POLYDACTYLOUS GENERATION.

Only one male, ♂ 3046 (tables 1 and 15), in this generation, has been extensively tested, and he has been used almost exclusively in matings with the best four-toed stock. His young in that sort of mating grade very high, viz 97, the standard of perfection being 100. He was mated to a female of class *N'* a single time, and produced three normal offspring and one polydactylous; these three were the only normal young he ever got in a total of ninety-two young. But this same mother bore to ♂ 1263 a litter of four young, *all polydactylous*. Facts like this indicate characteristic potencies on the part of gametes furnished by certain individuals, these potencies perhaps being handed on from generation to generation, as from ♂ 628 to his son, ♂ 1003.

7. INDIVIDUAL POTENCY VERSUS ANCESTRY.

The factor of gametic potency is evidently much greater than that of ancestry. For if we arrange the various sires in the order of the respective amounts of polydactylous ancestry which they possess (table 15), we see at once that this is not the order of their potencies, for those having the same amount of polydactylous ancestry often differ much in the potency with which they transmit the polydactyl character.

8. EXTRA-TOE OF LEFT SIDE BEST DEVELOPED.

The extra-toe, in the case of ♂ 23, was found on the left side of the body only. Among his descendants, also, the extra-toe, if present on one side of the body only, is more apt to be found on the left side. When the extra-toe is found on both sides of the body, but unequally developed, it is oftener the left side which has the better developed toe. The difference is not great, but is quite constant. Thus there have been recorded the following numbers of polydactylous feet: Left, 630; right, 589. These totals are made up from various partial sums given by different generations or families as follows:

														Total.
Left	61	66	51	41	18	98	112	21	51	34	24	53		630
Right	56	65	50	39	15	86	111	20	50	32	20	45		589

In every case the left toes slightly outnumber the right ones.

The extra-toes, as regards both degree of development and position on the body, are distributed as shown in table 16.

The extra-toe, it will be observed, occurs oftenest on the left side of the body, particularly in its higher grades of development (*G* and *F*).

The attempt has twice been made to increase by selection the asymmetry of the two sides of the body with reference to the extra-toe, but without success. The slightly superior development of the extra-toe on the left side of the body apparently remains unaffected. The cause of the asymmetry is unknown. The case doubtless belongs in the same category as the unequally developed right and left sex-glands of certain birds and mammals.

9. RESULT OF MATING NORMAL WITH POLYDACTYLOUS INDIVIDUALS.

Matings between normal females and polydactylous males have repeatedly been made, as will appear from tables 2 to 14. Crosses reciprocal to these have yielded the results indicated in table 17. The results, it will be seen, are not uniform. The offspring have, in some cases, a greatly weakened condition of the extra-toe, in other cases no extra-toe at all; in still other cases, the extra-toe may be present in a fairly well-developed condition. The inheritance is evidently neither sharply alternative (*i. e.*, Mendelian) nor completely blending. The result of a cross involving the extra-toe character is influenced by the individual potency of the respective parents. Fewer polydactylous young are produced if the normal parent comes of a stock in which the polydactylous character does not occur.

10. INHERITANCE NEITHER ALTERNATIVE NOR BLENDING.

It is very evident that in the inheritance of the extra-toe we are not dealing with a case of simple Mendelian dominance. An occasional case, like the matings of ♂ 628 with normal females (see table 4), would indicate that the extra-toe is a recessive character, but most polydactylous parents, in matings with normal individuals, give a mixture of normal with polydactylous offspring. Further, in these mixed lots of offspring, the polydactylous and normal individuals are rarely equal to each other in number, as we should expect if one parent were a Mendelian heterozygote, the other pure.

On the other hand, when two of the offspring produced by a cross between polydactylous and normal parents are mated together, we do get some evidence of Mendelian segregation. The offspring are highly variable as regards the character, extra-toe. Some are normal, some have poorly developed toes, and some have very well developed toes. The experiments are still incomplete as regards this matter, but so far do not indicate the formation of sharply separated Mendelian classes.

On the whole, it seems probable that the extra-toe is inherited in a manner intermediate between blending and alternative inheritance. The gametes only *partially* blend in the zygote, producing a variable result, most

often an intermediate condition. The gametes formed by the cross-breds are not homogeneous, as would be the case if complete blending occurred in the zygote, but are highly variable as regards the extra-toe. If the inheritance were sharply alternative, we should expect to get, not a series of graduated forms, but two or at most three sharply distinct groups, but this is not the observed result. If, on the other hand, inheritance were fully *blending*, all the offspring of two pure parents, or of two cross-bred parents, should be alike, but this is not the observed result. We are forced to conclude, therefore, that there occurs a *partial* blending of gametes in the zygote, and a *partial* segregation as the zygote gives off gametes.

Not improbably more characters fall in this category than in any other. Sharp alternative inheritance is comparatively rare, so is fully blending inheritance; most characters appear from generation to generation in a more or less well developed condition, not always strictly intermediate between the conditions found in the respective parents, nor always corresponding closely either with the condition found in one parent or with that found in the other. In dealing with such characters, selection must be the breeder's method of working. If he wishes either to eliminate or to "fix" a partially blending character he must make an appropriate choice of parents, not once nor twice, but many times over until the undesired condition ceases wholly to reappear.

It would be interesting to know in what condition characters like the extra-toe exist in the germ. It can not be in a state of simple recessiveness, for in that case the character should reappear in a Mendelian proportion of the offspring formed, but this, as we have seen, is not the case. More probably the character is present, active or inactive, in *every* gamete, but the conditions under which it may become active are too complex for present analysis. On the other hand, it is possible that *nothing* in the germ of a normal guinea-pig stands for the character, extra-toe, and that when this character is formed, it is formed *de novo*. But if so, we must account for the appearance of a new digit in the precise position of a lost one, and with all the appropriate nervous and muscular connections. This it seems quite as hard to do as to suppose an antecedent state of latency or inactivity of the character throughout certain generations of ancestors. Moreover, we have strong reasons for believing that, in color inheritance, specific pigments and specific color patterns may be transmitted unseen in a latent condition, often through long series of generations. If color characters are subject to transmission in a latent condition, it seems reasonable to suppose that other characters also may be transmitted in the same way.

TABLE 2.—*Character of the extra-toe in young of ♂ 23 (PN), of polydactylous generation I.*

Character of mother.	<i>G</i>	<i>F</i>	<i>P</i>	<i>N</i>	Total polydactylous individuals.	Total normal (<i>NN</i>) individuals.	Per cent. polydactylous.	Grade.
	<i>L R</i>	<i>L R</i>	<i>L R</i>	<i>L R</i>				
<i>G</i>								
<i>F</i>		2—1	—1		2	3	40	29
<i>P</i>			2—1	—1	2	2	50	19
<i>N</i>		4—5	2—2	3—2	9	27	25	17
<i>N'</i>			2—	—2	2	30	6	1.5
		6—6	6—4	3—5	15	62	19.5	22(?)

TABLE 3.*—*Character of the extra-toe in young of ♂ 193 (FF), generation II.*

Character of mother.	<i>G</i>	<i>F</i>	<i>P</i>	<i>N</i>	Total polydactylous individuals.	Total normal (<i>NN</i>) individuals.	Per cent. polydactylous.	Grade.
	<i>L R</i>	<i>L R</i>	<i>L R</i>	<i>L R</i>				
<i>G</i>	1—1	1—	—1		2	1	[67]	[55]
<i>F</i>	3—3	5—4		—1	8	2	80	58
<i>P</i>	6—5	10—7	2—4	1—3	19	5	79	57.5
<i>N</i>	5—4	3—2	4—7	4—3	16	26	38	22
<i>N'</i>		1—1	1—1	1—1	3	4	43	18.5
	15—13	20—14	7—13	6—8	48	38	56	46

TABLE 4.—*Character of the extra-toe in young of ♂ 628 (GF), generation III.*

Character of mother.	<i>G</i>	<i>F</i>	<i>P</i>	<i>N</i>	Total polydactylous individuals.	Total normal (<i>NN</i>) individuals.	Per cent. polydactylous.	Grade.
	<i>L R</i>	<i>L R</i>	<i>L R</i>	<i>L R</i>				
<i>G</i>	1—1	1—1			2		[100]	[90]
<i>F</i>			1—1		1	2	[33]	[17]
<i>P</i>	7—5	1—3	4—3	1—2	13	2	87	62
<i>N</i>						4	0	0
<i>N'</i>						8	0	0
	8—6	2—4	5—4	1—2	26	16	62	34

TABLE 5.—*Character of the extra-toe in young of ♂ 635 (FF), generation III.*

Character of mother.	<i>G</i>	<i>F</i>	<i>P</i>	<i>N</i>	Total polydactylous individuals.	Total normal (<i>NN</i>) individuals.	Per cent. polydactylous.	Grade.
	<i>L R</i>	<i>L R</i>	<i>L R</i>	<i>L R</i>				
<i>G</i>			2—1	—1	2	1	[67]	[25]
<i>F</i>	1—1	2—2			3		[100]	[87]
<i>P</i>	3—1	4—4	4—4	—2	11	7	78	40
<i>N</i>	3—2	8—8	11—7	1—6	23	32	42	24
<i>N'</i>		3—3	7—3	—4	10	24	29	14
	7—4	17—17	24—15	1—13	49	64	43	38

* In the last two columns of tables 3 to 13, per cent. or grades of the young, when based on a smaller number of individuals than four, are placed within brackets.

TABLE 6.—*Character of the extra-toe in young of ♂ 711 (GG), generation III.*

Character of mother.	G		F		P		N		Total polydactylous individuals.	Total normal (NV) individuals.	Per cent. polydactylous.	Grade.
	L	R	L	R	L	R	L	R				
G	7—	7	1—	1					8		100	97.5
F	2—	3	2—	2	3—	2			7	2	78	60
P	1—	1	2—	1	1—	2			4	3	57	42
N	1—	4	3—	1	3—	2	1—	1	8	8	50	33
N'			1—	1	4—	3	—	1	5	27	12.5	8
	11—	15	9—	6	11—	9	1—	2	32	40	44	48

TABLE 7.—*Character of the extra-toe in young of ♂ 809 (GG), generation III.*

Character of mother.	G		F		P		N		Total polydactylous individuals.	Total normal (NV) individuals.	Per cent. polydactylous.	Grade.
	L	R	L	R	L	R	L	R				
G	28—	24	4—	7	1—	3	1—		34	1	97	90
F	4—	4							4	1	80	80
P	4—	3	3—	3	2—	1	—	2	9		100	74
N	1—		—	1					1	1	[50]	[45]
N'	1—		1—	2	5—	4	1—	2	8	6	57	28
	38—	31	8—	13	8—	8	8—	8	56	9	86	63

TABLE 8.—*Character of the extra-toe in young of ♂ 954 (GG), generation IV.*

Character of mother.	G		F		P		N		Total polydactylous individuals.	Total normal (NV) individuals.	Per cent. polydactylous.	Grade.
	L	R	L	R	L	R	L	R				
G	9—	9	3—	3	6—	5	1—	2	19	2	90	67
F	3—	2	3—	4	1—	1			7	1	87.5	73
P	7—	5	7—	9	10—	10	2—	2	26	3	90	60
N	1—	3	2—		4—	5	1—		8	1	89	56
N'					1—		—	1	1	1	[50]	[12.5]
	20—	19	15—	16	22—	21	4—	5	61	8	88	54

TABLE 9.—*Character of the extra-toe in young of ♂ 1003 (FG), generation IV.*

Character of mother.	G		F		P		N		Total polydactylous individuals.	Total normal (NV) individuals.	Per cent. polydactylous.	Grade.
	L	R	L	R	L	R	L	R				
G	6—	6							6		100	100
F	3—	3	2—	1	—	2	1—		6	3	67	52
P												
N										20	0	0
N'												
	9—	9	2—	1	—	2	1—		12	23	34	51

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TABLE 10.—*Character of the extra-toe in young of ♂ 1140 (GN), generation IV.*

Character of mother.	G		F		P		N		Total polydactylous individuals.	Total normal (NN) individuals.	Per cent. polydactylous.	Grade.
	L	R	L	R	L	R	L	R				
G												
F	3—2		2—3		4—1		—3		9	2	82	48
P	4—2		3—3		4—4		1—3		12	3	80	49
N	3—2		2—2		—1				5	1	83	72.5
N'												
	10—6		7—8		8—6		1—6		26	6	81	56.5

TABLE 11.—*Character of the extra-toe in young of ♂ 1165 (GG), generation IV.*

Character of mother.	G		F		P		N		Total polydactylous individuals.	Total normal (NN) individuals.	Per cent. polydactylous.	Grade.
	L	R	L	R	L	R	L	R				
G	32—30		5—7		2—2				39	2	95	90
F	4—4		5—5		1—1				10		100	85
P	2—1				1—2				3	2	60	45
N					1—3		2—		3	7	30	10
N'												
	38—35		10—12		5—8		2—		55	11	83	50

TABLE 12.—*Character of the extra-toe in young of ♂ 1263 (GG), generation IV.*

Character of mother.	G		F		P		N		Total polydactylous individuals.	Total normal (NN) individuals.	Per cent. polydactylous.	Grade.
	L	R	L	R	L	R	L	R				
G	66—61		6—6		5—9		—1		77		100	93
F												
P	2—2								2	1	[67]	[67]
N												
N'	1—		3—4						4		100	82.5
	69—63		9—10		5—9		—1		83	1	99	81

TABLE 13.—*Character of the extra-toe in young of ♂ 1264 (GG), generation IV.*

Character of mother.	G		F		P		N		Total polydactylous individuals.	Total normal (NN) individuals.	Per cent. polydactylous.	Grade.
	L	R	L	R	L	R	L	R				
G	21—22		12—9		2—4		1—1		36	1	97.5	85
F	1—1		1—		—1				2		[100]	[82.5]
P	6—5		3—2		3—4		—1		12	2	86	66
N					2—2				2	4	33	17
N'										3	[0]	[0]
	28—28		16—11		7—11		1—2		52	10	84	50

TABLE 14.—*Character of the young of ♂ 3046 (GG), generation V.*

Character of mother.	<i>G</i>		<i>F</i>		<i>P</i>		<i>N</i>	Total polydactylous individuals.	Total normal (<i>NN</i>) individuals.	Per cent. polydactylous.	Grade.
	<i>L</i>	<i>R</i>	<i>L</i>	<i>R</i>	<i>L</i>	<i>R</i>	<i>L</i>	<i>R</i>			
<i>G</i>	79—77		8—8		1—2		—1	88	0	100	97
<i>N'</i>					1—		—1	1	3	25	8
	79—77		8—8		2—2		—1	89	3	97	

TABLE 15.—*Sires grouped by generations of polydactylous ancestry.*

[The numerals in parenthesis indicate rank in potency of transmission of the polydactylous character. Descent is shown in the male line only.]

Polydactylous generations in ancestry.	0	½	I	1½	2	2½	3
	23(5)	193(3)	711(3)	628(4) 635(4) 809(2)	1003(3) 1165(3) 1140(3) 1263(1) 1264(3)	954(3)	3046(1)
Generation (in male line).	I.	II.	III.		IV.		V.

TABLE 16.—*Frequency of occurrence of the extra-toe in its several degrees of development on the two sides of the body.*

	Left side.	Right side.	Per cent. left.
<i>G</i>	335	310	51.9
<i>F</i>	148	133	52.6
<i>P</i>	147	146	50.2
	630	589	51.6

TABLE 17.—*Character of the young produced by a mating between a normal (*N'*) male and females either polydactylous or of polydactylous ancestry.*

Father.	Character of mother.	<i>F</i>		<i>P</i>		<i>N</i>	Total polydactylous individuals.	Total normal (<i>NN</i>) individuals.	Per cent. polydactylous.	Grade.
		<i>L</i>	<i>R</i>	<i>L</i>	<i>R</i>	<i>L</i>				
♂ 482	<i>P</i>	1—		1—		—2	2	0	[100]	[32.5]
♂ 981	<i>F</i>			2—1		1—2	3	2	60	15
	<i>P</i>			2—3		1—	3	0	[100]	[25]
♂ 2054	<i>P</i>						0	4	0	0
	<i>N'</i>			—1		1—	1	5	17	4
♂ 2060	<i>G</i>	2—1		4—5			6	10	37.5	22
♂ 3609	<i>G</i>			2—1		—1	2	6	25	9

POSTSCRIPT.

A critical examination of the results obtained by Bateson, Punnett and Hurst (see Bateson, Saunders, Punnett and Hurst, :05) in poultry indicates that there too the inheritance of extra-toe is not strictly Mendelian, but corresponds with what I have found to be the condition in the *most potent* polydactylous sires. In poultry the extra-toe has been for a long time an established character of certain breeds. During all that time selection has undoubtedly been exercised in its favor, so that it is not surprising to find the character more strongly dominant than in my four-toed race of guinea-pigs. Nevertheless both Bateson and Hurst record cases in which polydactylous chicks are produced by normal parents of polydactylous ancestry.

Similar observations have repeatedly been made concerning the inheritance of polydactylism in man. See Ballowitz (:04) and Davenport (:04). Polydactylism usually makes its (recorded) appearance in some note-worthy form, is transmitted more or less strongly through two to five generations and then disappears, doubtless so weakened by repeated out-crosses that its manifestations, if any occur, are no longer observed.

Apparently it is only when selection is exercised for the polydactyl character and like individuals are mated to each other that a polydactylous race can be established. In its origin, polydactylism is a discontinuous variation or mutation, but without the aid of selection it would probably never become a racial character. Is not the same thing true of a great many of the characters which serve to distinguish the various races of domesticated animals and plants?

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